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HARPACTICOID COPEPODS (CRUSTACEA) OF THE FAMILY TETRAGONICIPITIDAE LANG: A REVIEW AND REVISION, WITH KEYS TO THE GENERA AND SPECIES

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In recent years there have been many new species and two new genera described in the Tetragonicipitidae. Most of these new forms are from tropical and semitropical areas (Por, 1964; Wells, 1967; Geddes, 1968a; Coull, 1969, 1970, 1971), which appears to be the evolutionary center for this family. Por (1964) has previously commented on the confused systematics of this family, the need for its revision, and on the increasing numbers of known taxa, particularly from tropical areas.

In this paper I include a revision (where necessary) to the genera in the family and provide keys to the known species. Some genera are little changed since the last complete review (Lang, 1948), while others (*Phyllopodopsyllus*, for example) have changed so much that even Lang's recent (1965) key to the genus is outdated. Except where publication lag misses new species, this review is complete (to my knowledge) and includes every species described up through October 1972.

This review is based entirely on the literature. I have tried to borrow and examine one of two species considered incerta sedis in this paper, i.e., *Phyllopodopsyllus pirgos* Apostolov 1969. However, I have met with no success in my attempts to borrow this species and am, therefore, unable to redescribe it as originally planned. The second incerta sedis species, *Phyllopodopsyllus tristanensis* Wiborg 1964 is lost (see Wiborg 1964, p. 34) and must await rediscovery before inclusion in any revision.

Each measurement used in this paper was recalculated by measuring the figures given in the original text. In caudal rami length/width ratios the width was measured at the widest portion of the ramus. The term caudal rami, not furca, is used after Bowman (1971). These measurements then, are not necessarily the same as listed by the authors or by those who cite the author, but are consistent throughout. The terminology used throughout is adopted from Lang (1948, 1965).

Family Tetragonicipitidae Lang 1948, Char. emend.

Tetragonicepsidae Lang 1948

Since Lang's (1948) familial diagnosis, several changes have been made, thus necessitating the following new diagnosis: Body elongate, more or less cylindrical. Female genital somite undivided dorsally. Caudal rami aberrant. Rostrum variable, from large and pointed to round and small to absent. Labrum very large. A_1 ♀ 5–9 segmented. A_2 with basis. Exp. A_2 1 segmented, with 1–3 setae. Md. well developed with 2–3 setae on coxa-basis and separate Exp., Enp. fused or distinct. Mx. with 4–5 endites. Mxp. well developed, prehensile. P_1 with 2–3 segmented Exp., when 3 segmented middle segment without inner seta; terminal segment with 3–5 setae. Enp. P_1 2–3 segmented, prehensile, 1st segment nearly as long as entire Exp. P_2–P_4 with 3 segmented Exp., 1–2 segmented Enp. Setation of P_2–P_4 variable. P_5 ♀ distinct or confluent. Single ovary. A_1 ♂ haplocer. P_2 or P_3 or P_4 or caudal rami may be dimorphic, or any combination of the above. ♂ P_5 always dimorphic. Benp. P_5 ♂ fused, Exp. and Benp. confluent or distinct.

Key to the Genera of Tetragonicipitidae

1. Cephalothorax with 2 pointed posterolateral processes ..... *Laophontella* Thompson & A. Scott 1903
   Cephalothorax without posterolateral processes 2
2. Exp. A_2 dwarfed, represented by a single seta ..... *Pteropsyllus* T. Scott 1906
   Exp. A_2 well developed with 2 or 3 setae 3
3. First segment A_1 with dentiform projection; Exp. P_5 ♂ 2-segmented 4
   First segment A_1 without dentiform projection; Exp. P_5 ♂ 1-segmented 5
4. Dentiform projection A_1 at posterior distal corner pointing laterally ..... *Tetragoniceps* Brady 1880
   Dentiform projection A_1 in middle of segment pointing medially ..... *Fearia* Coull 1971
5. First segment A_1 shorter than second ..... *Diagoniceps* Willey 1930
   First segment A_1 longer than second 6

6. Rostrum short, rounded; Benp. and Exp. P_5 ♀ confluent, foliaceous; Benp. P_5 ♂ with 3 setae ..... *Phyllopodopsyllus* T. Scott 1906
Rostrum as long as first 2 segments A_1, and pointed at tip; Benp. and Exp. P_5 ♀ distinct; Benp. P_5 ♂ with 2 setae ..... *Protogoniceps* Por 1964

Laophontella Thompson & A. Scott 1903

Type-species: *Laophontella typica* Thompson & A. Scott 1903

Phyllopodopsyllus armatus Willey 1935.—*Willeyella* Por 1964

Remarks: This genus, with its three species, has been extremely problematical in any attempts to elucidate Tetragonicipitidae systematics (see Willey, 1935; Sewell, 1940; Lang, 1948, 1965; Por, 1964; Bodin, 1967; Geddes, 1968a; Coull, 1969). I suspect that the description of the type of the genus (Thompson & Scott, 1903) is based on an immature female (e.g., bi-articulate P_5; uni-articulate P_4 endopod, short-stout antennae). The unifying feature of the three species is the pointed-cephalo-thoracic processes, a distinctive generic character. I, therefore, refer the reader to Por's (1964) generic designation of *Willeyella* (a junior synonym for *Laophontella*) for the diagnosis, keeping in mind that *L. typica* officially exists as the generic type, but that the original diagnosis may not be accurate.

Geddes (1968a) has further suggested that the description of *L. armata* var. *indica* Sewell may also be based on an immature form.

Generic diagnosis: See Por (1964, p. 105 for *Willeyella*)

Key to the Females of *Laophontella*

1. A_1 5 segmented 2
A_1 8 segmented, 1st segment prolonged with dentiform projection mid-way pointing medially; furca elliptical with spiniform projections laterally ..... *L. horrida* (Por)
2. P_5 foliaceous, comprised of single plate; 1st segment A_1 greatly elongated and slender so that it is as long as 4 succeeding segments combined: Enp. P_4 2 segmented ..... *L. armata* (Willey)
P_5 with distinct baseoendopodite and exopod, 1st segment A_1 broad, 2 times as long as 2nd segment, with small outer and inner projections; Enp. P_4 1 segmented ..... *L. typica* Thompson & A. Scott

Pteropsyllus T. Scott 1906, Char. emend.

Type-species: *Tetragoniceps consimilis* T. Scott 1894

Tetragoniceps T. Scott 1894

Remarks: Wells (1967) has recently reviewed this genus and suggests that it is monotypic, with *P. consimilis* (T. Scott, 1894) the only valid species. He asserts that *P. plebius plebius* Monard 1935, *P. plebius furcatus* Kunz 1938 and *P.* sp. Wells 1961 are all junior synonyms of

P. consimilis due to the continuous variations which exist. I see no need to alter Wells' (1967) conclusions and concur that the genus is indeed monotypic. No key is given as the generic key serves to distinguish the species.

Alteration to generic diagnosis: Lang's (1948, p. 890) generic diagnosis should be altered to state that P_6 ♂ is variable and may have confluent or distinct exopodite and baseoendopodite (after Wells 1967).

Tetragoniceps Brady 1880, Char. emend.

Type-species: *Tetragoniceps malleolatus* Brady 1880

Remarks: There are currently 10 valid species in this genus. Since the last review (Lang, 1948), the following species have been added: *T. truncata* and *T. longicaudata* Nicholls (1939), *T. arenicolous* Krishnaswamy (1957), *T. bergensis* Por (1965), *T. brownei* Wells (1967) and *T. bookhouti* Coull (1971). Table I summarizes the data on the known species. Male characteristics are not included as the males are known in only 4 of the 10 species. A key to the 10 known species is given below.

Alteration to generic diagnosis: Many species described subsequent to Lang's (1948) monograph do not fit his generic diagnosis, hence I present a new generic diagnosis: Caudal rami variable, ranging from as wide as long to 10 times longer than wide. Rostrum small or absent. A_1 ♀ 8–9 segmented, first segment elongate with dentiform projection at posterior distal corner pointing laterally. Exp. A_2 well developed, with 2 or 3 setae. Enp. Mxl. well developed. Mx. with 4 or 5 endites. Enp. P_1 2 segmented. Setal formulae variable (see Table I). P_5 ♀ confluent or distinct. Setation on P_5 ♀ variable. P_5 ♂ distinct in all known species. Sexual dimorphism in P_2 or P_2 and P_3, or caudal rami. A_1 ♂ with or without dentiform projection.

Key to the Females of *Tetragoniceps*

1. P_5 fused into single plate each side 2
   P_5 not fused into single plate each side 4
2. Exp. A_2 with 3 setae 3
   Exp. A_2 with 2 setae ..... *T. bookhouti* Coull
3. Exp. portion P_5 with only 1 well-developed seta .. *T. malleolatus* Brady
   Exp. portion P_5 with 4 well-developed setae .....
   ..... *T. dubius* Thompson & A. Scott
4. *C.R. 3 times as long as wide 5
   *C.R. at most 2 times as long as wide 7
   *C.R. 10 times as long as wide; cephalothorax with dorsal dentiform projection ..... *T. bergensis* Por
5. Middle segment Exp. P_3–P_4 with inner seta 6
   Middle segment Exp. P_3–P_4 without inner seta .....
   ..... *T. longicaudata* Nicholls

TABLE 1. Genus *Tetragoniceps*—Summary of salient female morphological characters

Species	A_1 No. seg.	No. setae Exp. A_2	P_5—Benp. & Exp.	No. setae P_5 Benp.	No. setae P_5 Exp.	Caudal rami length/ width	Setal formulae P_2 Exp.	P_2 Enp.	P_3 Exp.	P_3 Enp.	P_4 Exp.	P_4 Enp.
malleolatus Brady	8	3	confluent	4(5)	1	?	unknown		0.1.022	?.121	0.1.221	1.120
dubius Thompson & A. Scott	8	3	confluent	5	4	1:1	unknown		unknown		1.1.322	1.020
bookhouti Coull*	8	2	confluent	4(5)	4	4:1	0.1.122	1.120	0.1.122	1.120	0.1.122	1.120
brevicauda T. Scott	9	3	distinct	5	6	1.5:1			unknown			
scotti Sars*	9	3	distinct	4	6	3:1	unknown		1.1.122	1.120	1.1.123	1.120
truncata Nicholls	9	3	distinct	4(5)	6	1:1 (truncate)	1.0.023	1.120	1.0.023	1.120	1.1.223	1.120
longicaudata Nicholls	9	3	distinct	3	5	3:1	1.0.023	1.120	1.0.023	1.120	1.1.123	1.020
arenicolous Krishnaswamy	8	2	distinct	4	3	3:1	1.1.023	1.020	? 1.023	unknown	1.1.123	1.121
bergensis Por*	9	3	distinct	4	5	10:1	0.1.222	1.120	0.1.221	1.120	0.1.223	1.120
brownei Wells*	8	3	distinct	5	4	2:1	1.0.022	1.020	1.0.221	1.020	1.0.221	1.020

* Designates species in which the male is known.

6. Exp. P_5 with 3 setae; last segment Exp. P_3 with 3 outer setae; Exp. A_2 with 2 setae ..... *T. arenicolous* Krishnaswamy
   Exp. P_5 with 6 setae; last segment Exp. P_3 with 2 outer setae; Exp. A_2 with 3 setae ..... *T. scotti* Sars
7. Exp. P_5 with 6 setae 8
   Exp. P_5 with 4 setae; Fu. with prominent dorsal keel; dentiform projection A_1 small ..... *T. brownei* Wells
8. *C.R. truncate, broad at somitic attachment, rapidly compressed ..... *T. truncata* Nicholls
   *C.R. normal, gradually tapering ..... *T. brevicauda* T. Scott

* C.R. refers to caudal rami

Fearia Coull 1971

Type-species: *Fearia prima* Coull 1971

Remarks: This monotypic genus is characterized by the medially pointing dentiform projection on the first segment of the female and male A_1. There is but one species in the genus, *F. prima*. The generic diagnosis must still be considered preliminary as it is based solely on the type-species (Coull, 1971). Except for the antennule spine, *Fearia* is very close to *Tetragoniceps*.

Diagoniceps Willey 1930, Char. emend.

Type-species: *Diagoniceps laevis* Willey 1930

Remarks: Since Lang's (1948) review of this genus, two species have been added, *D. monodi* Chappuis and Kunz (1955) and *D. menaiensis* Geddes (1968b), bringing to four the number of known species. Geddes (1968b) has discussed his unique species and compared it with the others in the genus. The 3-segmented P_1 makes *D. menaiensis* an enigma. For the time being, however, I agree with Geddes (1968b) and prefer to leave the species in *Diagoniceps* rather than create a new genus for it.

Alteration to generic diagnosis: With the addition of *D. monodi* and *D. menaiensis*, Willey's (1930, p. 94–95) and Lang's (1948, p. 894) generic diagnosis must be changed as follows: P_1 of 2 or 3 segments; Exp. P_5 ♀ with 5 or 6 setae.

Key to the Females of *Diagoniceps*

1. Enp. P_1 2 segmented 2
   Enp. P_1 3 segmented ..... *D. menaiensis* Geddes
2. Inner edge of *C.R. with small rounded projection: terminal segment exopod P_4 with 2 inner setae ..... *D. laevis* Willey
   Inner edge of *C.R. straight, terminal segment exopod P_4 with 3 inner setae 3
3. Terminal segments exp. P_2–P_4 with 3 outer setae ..... *D. bocki* Lang
   Terminal segments exp. P_2–P_4 with 2 outer setae ..... *D. monodi* Chappuis & Kunz

* C.R. refers to caudal rami

Phyllopodopsyllus T. Scott 1906, Char. emend.

Type-species: *Tetragoniceps bradyi* T. Scott 1892

Tetragoniceps T. Scott 1892

Paraphyllopodopsyllus Lang 1948

Remarks: Since Lang's (1965) revision and key, the following species have been added. *P. danielae* Bodin (1964); *P. tristanensis* Wiborg (1964); *P. biarticulatus* Wells (1967); *P. ponticus* Apostolov (1968); *P. bahamensis* Geddes, *P. opististoceratus* Geddes; *P. parafurciger* Geddes (1968a), *P. pirgos* Apostolov (1969), *P. hermani* Coull (1969), *P. chavei* Coull, *P. paraxenus* Coull (1970), *P. parafurciger carolinensis* Coull (1971). The female of *P. longicaudatus* A. Scott has been described by Vervoort (1964) and Marinov (1971) has redescribed the females of *P. briani* Petkovski and *P. thiebauldi* Petkovski. Challis (1969) mentions *Phyllopodopsyllus* sp. from the Solomon Islands, but there is no description available to date.

Lang (1965) has recently discussed the genus and divided it into three groups: (1) with a strong unguiform projection on the second segment of A_1; (2) with a small, but not unguiform projection on segment 2 of A_1; and (3) with no projection on segment 2 of A_1. This third group had previously been designated a separate genus, *Paraphyllopodopsyllus*, but Lang (1965) asserts that the 2 genera cannot be kept apart, especially when one considers the many intermediate forms, and concluded that *Paraphyllopodopsyllus* must be withdrawn. This is the format that will be followed here; i.e., one genus with three groupings within the genus.

Table 2 lists the salient features for all the known species. Two recently described species (*P. tristanensis* and *P. pirgos*) deserve further evaluation. *P. tristanensis* is a taxonomic nightmare because the critical swimming legs are not included and the characters listed by Wiborg (1964) are of little taxonomic value. The description of *P. pirgos*, I suspect, is based on an immature (5th copepodite) male. This is particularly evident in Apostolov's (1969) figures of the swimming legs (the segments of which appear too broad and indistinct for the adult and show no sexual dimorphism) and the P_5 which is still in the fused state. Nowhere else in the genus does a fused P_5 occur although I have observed a similar morphology in stage 5 copepodites of my *P. hermani*. Furthermore, Apostolov (1969) does not figure or refer to the antennule (especially the critical unguiform process) except to mention that it is eight segmented. He then goes on to distinguish his *P. pirgos* from *P. briani* and *P. thiebauldi* on the number of antennule segments. However, he has compared the A_1 of his male specimens to the A_1 of Petkovski's (1955) female specimens. Apostolov's species (*P. pirgos*) must therefore be considered incerta and await redescription. Since Wiborg's species (*P. tristanensis*) is known only from his incomplete drawings and the types are lost, it too must be considered incerta sedis. Neither of

TABLE 2. Genus *Phyllopodopsyllus*—Summary of salient morphological characters. + or – in column listed C.R. dorsal keel, refers to the presence (+) or absence (–) of a dorsal keel.

	Female										Male			
					Seta formulae						No. setae			
					P_2		P_3		P_4		P_5			
Species	No. seg. A_1	C.R. L/W ratio	C.R. 1° terminal seta	C.R. dorsal keel	Exp.	End.	Exp.	End.	Exp.	End.	Benp.	Exp.	C.R. ratio	C.R. dorsal keel
Process A_1 large														
bermudae Lang	8	7.1	bulbous	—	1.0.122	0.3	1.0.222	0.3	1.1.322	1.3	3	5	8.5	—
bradyi (T. Scott)	9	1.4	bulbous	—	1.0.122	0.3	1.0.222	1.3	1.1.321	1.3	3	5	5.5	—
parabradyi Lang	9	1.4	bulbous	—	1.0.122	1.3	1.0.122	1.2	1.1.222	1.3	3	5	5.2	—
minutus Lang	8	5.6	non-bulbous	—	1.0.122	0.3	1.0.222	0.3	1.1.222	1.2	3	5	?	?[1]
furciger Sars	8	3.3	bulbous	+	1.0.122	0.3	1.0.222	1.3	1.1.322	1.3[2]	3	5	5.5	—[2]
aff. *furciger* Por	8[3]	3.0	bulbous	+	1.0.122	0.3	1.0.222	0.3	1.1.221	1.3		unknown		
borutzkyi Lang	9	2.0	bulbous	—	1.0.022	0.3	1.0.022	1.3	1.0.222	1.3	3	5	3.9	—
pauli Crisafi	8	1.6	bulbous (modified)	—	1.0.022	1.3	1.0.022	1.3	1.1.222	1.3	3	5	4.4	—
medius Por	8[4]	2.0	bulbous	—	1.0.022	0.3	1.0.022	0.3	1.0.221	1.3	3	5	3.5	—
laticauda Por	8[4]	1.4	bulbous	—	1.0.022	0.3	1.0.022	0.3	1.1.221	1.3		unknown		
minor (Thompson & A. Scott)	8	3.8	non-bulbous	—	"Legs much the same as *bradyi*"							unknown[5]		
danielae Bodin	8	2.0	bulbous (modified)	—	1.0.022	1.3	1.0.022	1.3	1.0.322	1.3	3	5	2.8	—
chavei Coull	8	3.0	bulbous	—	1.0.122	1.3	1.0.222	1.3	1.1.222	1.3	3	5	unknown	
hermani Coull	9	3.1	non-bulbous	—	1.0.022	0.2	1.0.022	1.2	1.0.221	1.1	3	5	4.5	—
bahamensis Geddes	9	2.0	bulbous	+	1.0.022	0.3	1.0.022	0.3	1.0.222	1.2		unknown		
opistoceratus Geddes	9	3.2	non-bulbous	—	1.0.022	0.3	1.0.022	0.3	1.0.222	3	3	5	5.9	—
longicaudatus A. Scott	9	5.1	bulbous	—	1.0.122	0.3	1.0.222	1.3	1.1.222	1.3	3	5	8.0	—[6]

[1] Willey (1935) does not mention or figure the male caudal rami.
[2] Setal formula, male information from Bodin (1964).
[3] Por (1964) does not mention the A_1, but I assume it's the same as *furciger*.
[4] Por (1964) does not mention A_1 in text; information from Por (pers. comm.).
[5] Lang (1965) lists the male of *minor* as known; however, I cannot find the male description anywhere in the literature.
[6] Male information from Vervoort (1964).

TABLE 2. *Continued.*

Species	Female: No. seg. A_1	C.R. L/W ratio	C.R. 1° terminal seta	C.R. dorsal keel	Setal formulae: P_2 Exp.	P_2 End.	P_3 Exp.	P_3 End.	P_4 Exp.	P_4 End.	Male: No. setae P_5 Benp.	P_5 Exp.	C.R. ratio	C.R. dorsal keel
parafurciger parafurciger Geddes	8	2.2	bulbous	—	1.0.122	0.3	1.0.222	1.3	1.1.322	1.3	3	5	7.3	—[7]
parafurciger carolinensis Coull	8	2.1	bulbous	—	1.0.122	0.3	1.0.222	1.3	1.1.322	1.3	3	5	7.3	—[7]
Small process A_1														
briani Petkovski[8]	9	4.0	non-bulbous	+	1.0.122	1.3	1.0.222	1.3	1.1.322	1.3	3	5	4.0[9]	+?[9]
hardingi (Roe)	9	2.7	non-bulbous	—	1.0.022	1.3	1.0.022	1.3	1.0.321	1.3	3	5	?[10]	—?[10]
No process A_1														
aegypticus Nicholls	9	1.6	non-bulbous	—	1.0.122	0.3	1.0.222	0.3	1.1.321	1.3		unknown		
thiebauldi Petkovski	9	1.6	non-bulbous	+	1.0.122	1.3	1.0.122	1.3	1.1.3–222	1.3	3	5	3.2	—
mossmani T. Scott	9	2.5	bulbous	+	1.0.022	1.3	1.0.122	1.3	1.0.322	1.3	3	5	2.2	—
paramossmani Lang	9	2.0	non-bulbous	?	1.0.022	1.3	1.0.022	1.3	1.0.222	1.3	3	5	?[11]	?[11]
berrieri Monard	9	3.3	non-bulbous	—	1.0.022	1.3	1.0.022	1.3	1.0.223?	1.3	3	5	4.7	—[12]
hibernicus (Roe)	9	1.3	non-bulbous	+	1.0.022	1.3	1.0.022	1.3	1.0.322	1.3		unknown		
xenus (Kunz)	9	2.1	non-bulbous	—	1.0.022	0.2	1.0.022	0.2	1.0.321	0.3		unknown		
paraxenus Coull	8	1.6	bulbous	+	1.0.022	0.2	1.0.022	0.2	1.0.321	0.2	3	5	2.0	—
ponticus Apostolov	9	2.0	non-bulbous	—	1.0.022	1.3	1.0.022	1.3	1.0.122	1.3	3	5	5.0	—
longipalpatus (Chappuis)	8	1.5	non-bulbous	—	1.0.022	0.2	1.0.022	0.2	? ? 321	1.2	3	4	3.1	—
biarticulatus Wells[13]	8	1.4	non-bulbous	+	1.0.022	0.2	1.0.022	0.2	1.0.222	0.2	3	4	2.2	+[13]
tristanensis Wiborg[14]	9	2.5	non-bulbous	?			unknown				3	5	3.1	—

[7] These 2 subspecies are separated on presence or absence of protuberance on inner margin of the caudal rami.

[8] Marinov (1971) does not figure the small process on the second antennal segment.

[9] Petkovski (1955) says the caudal rami the same as the female.

[10] Roe (1955) states caudal rami same as female, but smaller.

[11] Lang (1934) gives no figures, but states male caudal rami same as female.

[12] Male information from Pesta (1959).

[13] Wells' (1967) species is distinguished from all the others in the genus by a 2-segmented P_1 Exopodite and a small dorsal keel on the male caudal rami.

[14] This species is considered incertae sedis (see text).

these species is included in the key, although *P. tristanensis* is included in Table 2.

Since several males are unknown or very poorly described, the following key to the valid species is based on the females.

Alteration to generic diagnosis: Since Lang (1965) combined *Paraphyllopodopsyllus* with *Phyllopodopsyllus*, a new generic diagnosis has not been made and is required.

Generic diagnosis: Caudal rami aberrant, generally longer than wide. Rostrum small, separated from body. A_1 ♀ 8–9 segmented, 1st segment longer than second. 2nd segment with or without dentiform projection. Exp. A_3 well developed with 3 setae. Mxl. with separate Exp. and Enp. Mx. with 5 endites. Enp. P_1 2-segments; Exp. P_1, 2–3 segments. Exp. P_2–P_4, 3 segments, Enp. P_2–P_3, 2 segments; Enp. P_4, 1–2 segments. P_5 ♀ large, foliaceous, Benp. and Exp. fused into single leaf-shaped plate. P_5 ♂ with distinct Benp. and Exp., Benp. with 3 setae, Exp. with 4–5 setae. P_2 or P_2 and P_3 dimorphic. ♂ caudal rami aberrant, may or may not be different than ♀, always longer than wide.

Key to the Females of *Phyllopodopsyllus*

1. Second segment A_1 with a conspicuous unguiform process 2
   Second segment A_1 with a small not unguiform process 20
   Second segment A_1 without any process 21
2. A_1 of 9 segments 3
   A_1 of 8 segments 9
3. *C.R. with a large conspicuous lamellar expansion inside near base 4
   C.R. with no or very slight lamellar expansion inside near base .. 5
4. 1st segment Enp. P_2 without seta, last segment Enp. P_3 with 3 setae; last segment Exp. P_3 with 6 setae ..... *P. bradyi* (T. Scott)
   1st segment Enp. P_2 with seta, last segment Enp. P_3 with 2 setae; last segment Exp. P_3 with 5 setae ..... *P. parabradyi* Lang
5. Principal terminal seta *C.R. not bulbous at base. 6
   Principal terminal seta *C.R. bulbous at base 7
6. Enp. P_4 1-segmented with 3 setae ..... *P. opistoceratus* Geddes
   Enp. P_4 2-segmented; last segment with one seta .. *P. hermani* Coull
7. *C.R. about 2 times as long as wide; last segment Exp. P_2–P_3 with 4 setae 8
   *C.R. 5 times as long as wide; last segment Exp. P_2–P_3 with 5 and 6 setae respectively ..... *P. longicaudatus* A. Scott
8. *C.R. without dorsal keel; 1st segment Enp. P_3 with inner seta; last segment P_4 with 3 setae ..... *P. borutzkyi* Lang
   *C.R. with dorsal keel; 1st segment Enp. P_3 without inner seta; last segment Enp. P_4 with 2 setae ..... *P. bahamensis* Geddes
9. Principal terminal seta *C.R. not bulbiform at base 10
   Principal terminal seta *C.R. bulbiform at base 11
10. *C.R. 5.6 times as long as wide; inner edge *C.R. straight and hairy ..... *P. minutus* Lang

*C.R. 3.8 times as long as wide; inner edge *C.R. slightly convex and not haired ..... *P. minor* (Thompson & A. Scott)

11. 1st segment Enp. P_2 with inner seta 12
    1st segment Enp. P_2 without inner seta 14
12. Last segment Exp. P_2–P_3 with 4 setae; principal terminal seta C.R. short and modified as bulb 13
    Last segment Exp. P_2–P_3 with 5 and 6 setae respectively; principal terminal seta C.R. also bulbous but with long slender spine protruding distally ..... *P. chavei* Coull
13. Last segment Exp. P_4 with 7 setae; middle segment Exp. P_4 without inner seta ..... *P. danielae* Bodin
    Last segment Exp. P_4 with 6 setae; middle segment Exp. P_4 with inner seta ..... *P. pauli* Crisafi
14. *C.R. at most 3–4 times as long as wide 15
    *C.R. 7–8 times as long as wide ..... *P. bermudae* Lang
15. Last segment Exp. P_2–P_3 with 4 setae 16
    Last segment Exp. P_2–P_3 with 5 and 6 setae respectively 17
16. Middle segment Exp. P_4 with inner seta; total body length > 1 mm ..... *P. laticauda* Por
    Middle segment Exp. P_4 without inner seta; total body length 0.6–0.85 mm ..... *P. medius* Por
17. *C.R. without dorsal keel—*P. parafurciger* 18
    *C.R. with dorsal keel—*P. furciger* 19
18. *C.R. with pointed knob like inner protrusion at ½ the length ..... *P. parafurciger parafurciger* Geddes
    *C.R. convex along inner margin with no distinctive knob like protrusion ..... *P. parafurciger carolinensis* Coull
19. Last segment Exp. P_4 with 5 setae and spines in all ..... *P.* aff. *furciger* Por
    Last segment Exp. P_4 with 7 setae and spines in all (according to Bodin 1964) ..... *P. furciger* Sars
20. *C.R. 4 times as long as wide with dorsal hairy keel; last segment Exp. P_3–P_4 with 6 and 7 setae respectively ..... *P. briani* Petkovski
    *C.R. 2.5–3 times as long as wide; no dorsal keel; last segment Exp. P_3–P_4 with 4 and 6 setae respectively ..... *P. hardingi* (Roe)
21. A_1 of 8 segments, Exp. P_5 (♂) with 4 setae 22
    A_1 of 9 segments, Exp. P_5 (♂) with 5 setae 23
22. Exp. P_1 3 segmented, last segment with 4 setae ..... *P. longipalpatus* (Chappuis)
    Exp. P_1 2 segmented, last segment with 5 setae ..... *P. biarticulatus* Wells
23. Principal terminal seta of *C.R. bulbous at base 24
    Principal terminal setae of *C.R. not bulbous at base 25
24. Last segment Enp. P_2–P_4 with 2 setae; C.R. with no inner expansion in proximal half, *C.R. 1.5 times as long as wide ..... *P. paraxenus* Coull

Last segment Enp. P_2–P_4 with 3 setae; C.R. with inner expansion in proximal half; *C.R. 2.5 times as long as wide ..... *P. mossmani* T. Scott

25. 1st segment Enp. P_2–P_3 without inner seta 26
    1st segment Enp. P_2–P_3 with inner seta 27
26. Last segment Enp. P_2–P_3 with 3 setae ..... *P. aegypticus* Nicholls
    Last segment Enp. P_2–P_3 with 2 setae ..... *P. xenus* (Kunz)
27. *C.R. with inner and outer lamellar expansions at base ..... *P. thiebauldi* Petkovski
    *C.R. without expansions at base 28
28. Last segment Exp. P_4 with 7 setae 29
    Last segment Exp. P_4 with 6 setae ..... *P. paramossmani* Lang
    Last segment Exp. P_4 with 5 setae ..... *P. ponticus* Apostolov
29. *C.R. 3.3 times as long as wide, distal inner edge slightly concave, *C.R. without dorsal keel ..... *P. berrieri* Monard
    *C.R. 1.3 times as long as wide, analoperculum hairy on distal edge, *C.R. with dorsal keel ..... *P. hibernicus* (Roe)

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* C.R. refers to caudal rami

Protogoniceps Por 1964

Remarks: Since Por's (1964) creation of the genus, no new species have been added. It is very difficult to ascertain the validity and/or the primary characteristics of the genus from Por's original description since his text and figures contradict each other. Lang (1965, p. 386) has already pointed out the discrepancy between the number of setae on the last exopodite segment of P_1 (i.e., Por's text says 5 setae, yet he illustrates 4). Furthermore, Por (1964) states that "the endopodite of P_1 is formed of 2 segments," yet his Plate 19, Figure 211 shows the P_1 endopodite as 3 segmented.

Recently, Dr. Por sent his original figures (Por, pers. comm., 30 May, 1972) and it is obvious that mistakes were made in drafting and typing. The terminal segment of the P_1 exopodite has 4 setae and the P_1 endopodite is composed of 2 segments, thus clarifying the published discrepancies.

Por relates some features of *Protogoniceps* to *Pteropsyllus*, some to *Tetragoniceps* and some to *Phyllopodopsyllus*. With the descriptions of several new species and familial revisions (Lang, 1965; Wells, 1967), these relationships are no longer valid. For example, the 9-segmented A_1 and "primitive" P_5 (♀ or ♂?) does not necessarily relate *Protogoniceps* to *Tetragoniceps* as one-half the known *Tetragoniceps* have 8-segmented antennules and 3 of the known species have a confluent, not distinct ("primitive") ♀ P_5. *Pteropsyllus* is known to harbor much variation within its single species (Wells, 1967) and setal formulae affinities between it and *Protogoniceps* may well be within the range of specific variation and lends no support to the relationship of these two genera.

Por (1964) states that *Protogoniceps* and *Phyllopodopsyllus* are related by the presence of the spur on second antennular segment. Lang (1965) has refuted the spur as a generic characteristic, and many known *Phyllopodopsyllus* completely lack the spur or have it in a greatly reduced condition (Table 2). It is, therefore, impossible to relate *Protogoniceps* to any of the known Tetragonicipitidae, but hopefully with continued collection more specimens will be collected and the intergeneric relationships elucidated.

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